

MORPHOLOGY AND ANATOMY OF
CROOMIA PAUCIFLORA (STEMONACEAE)

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THE STEMONACEAE (Roxburghiaceae) comprises a small and taxonomically isolated family of monocotyledons with its main distribution in the Far East. *Stemona* ranges from the Himalayas to southern Australia and *Stichoneuron* is found in Indonesia. The remaining genus *Croomia* (commemorating the pioneer Florida botanist H. B. Croom), has a widely disjunct range with two species in Japan and one (*C. pauciflora* Torr.) in the southeastern United States. This family therefore provides a further example of distribution demonstrating the ancient floristic affinity between eastern North America and eastern Asia to which Asa Gray drew attention.

There is little agreement amongst taxonomists as to where in a natural sequence the Stemonaceae should be situated. Burkill (1960) provides a useful survey of the taxonomic history of the family. Its wide and discontinuous distribution has led to the assumption that it is ancient (Hutchinson, 1959) but there is much evidence that the taxon is not very homogeneous. Any information likely to shed light on the systematics of the family is therefore of value, especially in view of its possible relationship with the economically important Dioscoreaceae. Recently one of us (P. B. T.) had the opportunity to collect *Croomia pauciflora* in northern Florida and to investigate its morphology and anatomy with ample fresh material at hand. The other (E. S. A.) has investigated the vegetative anatomy of the three genera and the total contribution permits a discussion of their systematic affinities. Only limited herbarium material of *Stichoneuron* and *Stemona* has been available for microscopic investigation, and observations on these two genera are still very tentative. The vegetative anatomy of *Croomia pauciflora* was investigated previously by Holm (1905) with some of the information repeated in a later paper (Holm, 1927), but it is quite clear that many fundamental morphological features have hitherto remained undescribed. They are presented in this paper, together with a detailed re-examination of anatomy. In addition the anatomy of the flower has been studied in order to compare it with that of *Stemona* about which there is a good deal more information.

In the United States *Croomia* grows on richly wooded bluffs along the Apalachicola River from Florida into Alabama (Harper, 1942). Plants form small, very localized populations in dense shade on steep, well-drained

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slopes amongst loose litter. According to Harper they remain green all summer. Populations seem to persist and spread largely by rhizomes which are, however, shallow and easily dug up. We have not seen any seedlings. Harper spoke of plants being "more or less connected by a network of rootstocks." This is substantiated by the abrupt boundary to the populations and the high density of leafy shoots. Rhizome morphology described below accounts for this method of vegetative survival but also suggests that *Croomia* would be vulnerable to any disturbance of its habitat.

MATERIAL AND METHODS

Living plants came from Torreya State Park, Bristol, Florida. We are indebted to Dr. S. McDaniels and Dr. A. F. Clewell of Florida State University for the arrangements made so that specimens could be collected. Plants were examined largely in a fresh condition. Microscopic details were studied in unstained freehand sections cut with a razor blade, supplemented by observations on preparations made by routine clearing, staining, and maceration methods. Details of the vascular system were examined in serial sections of paraffin-embedded material stained in safranin and Delafield's haematoxylin. The vascular anatomy of open flowers and mature flower buds was studied in serial paraffin sections and in whole flowers cleared and stained in safranin. A number of foliage leaves were cleared and stained in Heidenhain's haematoxylin.

Material of *Stichoneuron* and *Stemona* from the Herbarium, Royal Botanic Gardens, Kew, as follows, was supplied through the generosity of Dr. C. R. Metcalfe, Keeper of the Jodrell Laboratory: *Stemona curtisii* Hook. f. (*Haniff & Nur* 4368); *S. kerrii* Craib (*Kerr* 707); *Stichoneuron caudatum* Ridley (*Corner* 28716 & 37056).

VEGETATIVE MORPHOLOGY

GROWTH HABIT (FIGS. 35–39). Growth of shoots is sympodial with a remarkably precise and constant arrangement of parts on each unit of the sympodium. Each of these units consists of an underground rhizomatous portion terminating in an erect leafy shoot which bears the flowers (FIG. 35). At the time of flowering, in March to April, the renewal shoot has already been initiated (FIG. 37) for the next unit which will culminate in the following year's erect shoot. Leafy shoots are, therefore, annual but the slender rhizomatous part of the sympodium is long persistent and marked by the scars of each erect shoot. These scars therefore represent the limit of each annual growth increment. Long rhizomes with many scars can be dug up easily.

Each unit of the sympodium begins with a series of scale leaves. Their position and number are so constant from year to year that they may be identified by letters for convenience (FIGS. 35, 37). Leaves are arranged distichously (FIG. 38). The plane of distichy is horizontal although this is interrupted once in a very significant way. The following

sequence is standard for each renewal shoot. The first leaf (A) is a scale leaf at the end of a long internode; it subtends no axillary bud. Leaf B is a scale leaf opposite leaf A and also at the end of a long internode. It subtends a conspicuous bud which is, however, strongly inhibited (*dormant bud*, FIG. 39). Leaf C is a scale leaf at the end of a short internode and inserted on the dorsal (lower) side of the rhizome and therefore perpendicular to the plane of distichy of leaves A and B. Leaf C subtends the bud which grows out, without inhibition, as the renewal shoot (*renewal bud*). Beyond leaf C the axis turns erect (FIG. 37). Three (sometimes only two) overlapping scale leaves (D, E or F) separated by short internodes are inserted at the base of the erect shoot. These re-establish the earlier distichy so that D is always on the same side of the shoot as B. The last scale leaf (E or F) is often somewhat remote from the other two and its apex is usually above ground. The extent to which the internode below the last scale leaf is elongated and whether two or three scale leaves occur beyond leaf C may be determined by the depth to which the rhizome is buried. These 2 or 3 ultimate scale leaves subtend no conspicuous buds although microscopical examination of sections through their nodes sometimes reveals vestigial buds with little or no vascular connection to the main vascular system. These may be described as *non-functional* buds since they never seem to expand and are in sharp contrast to the conspicuous *functional* buds at nodes B and C which have a strong connection to the main vascular system of the rhizome.

Beyond the last scale leaf (E or F) is the long internode, up to 30 cm. tall, which supports the leafy crown. This internode is white below ground but exposed parts are red below and green above. The exposed apex of the distal scale is also red. Foliage leaves from a terminal, irregular, obliquely ascending series spreading backwards more or less in one plane and apparently continuing the distichy of the scale leaves although they are irregularly spaced and often subopposite (FIG. 36). The axis of the whole sympodium is apparently terminated by a leaf or pseudo-pair of leaves. Vigorous shoots bear as many as nine leaves, from five to seven are the most common numbers. Small shoots may have as few as two or three foliage leaves but we have seen no shoot with one leaf. Flowering branches are in the axils of leaves. In non-flowering shoots there may be vestigial axillary buds.

From the above description it is evident that branching is very restricted. Each sympodial unit bears only two functional buds (FIG. 38), one (renewal bud) is necessary to maintain the sympodium, leaving only one (dormant bud) to effect multiplication by branching. At the time of anthesis the renewal bud has usually commenced growth, piercing the back of its subtending scale leaf (FIG. 37). At this stage the primordia of the first two scale leaves of next year's increment are already present but they so firmly enclose the bud that its apex appears to be naked and leafless. Examination of herbarium specimens collected in the fall suggest that the rhizome overwinters with a full complement of leaves initiated.

In contrast, the dormant bud is strongly inhibited because many rhi-

zomes remain undivided even after several years' growth. However, divided rhizomes, in which the dormant bud has grown out to initiate a new sympodium, are quite common. Normally this branch axis repeats the arrangement of parts shown on the parent axis and produces a vigorous but flowerless leafy shoot in the first year. Commonly, however, the lateral shoot is not vigorous and the first two internodes remain unextended so that a short, depauperate leafy shoot with few (2-3) foliage leaves is erected close to the parent axis. Although it is reasonable to assume that damage to a vigorous renewal shoot will release inhibition of dormant buds, most branched rhizomes appear undamaged. Therefore, it is not easy to account for the outgrowth of dormant buds which otherwise are strongly suppressed.

Roots are restricted to the nodes at which leaves B and C are inserted, from three to five growing out adventitiously on the lower side of the rhizome (FIGS. 35, 37). Roots are somewhat fleshy and produce a fine system of first-order branches but without conspicuous root-hairs.

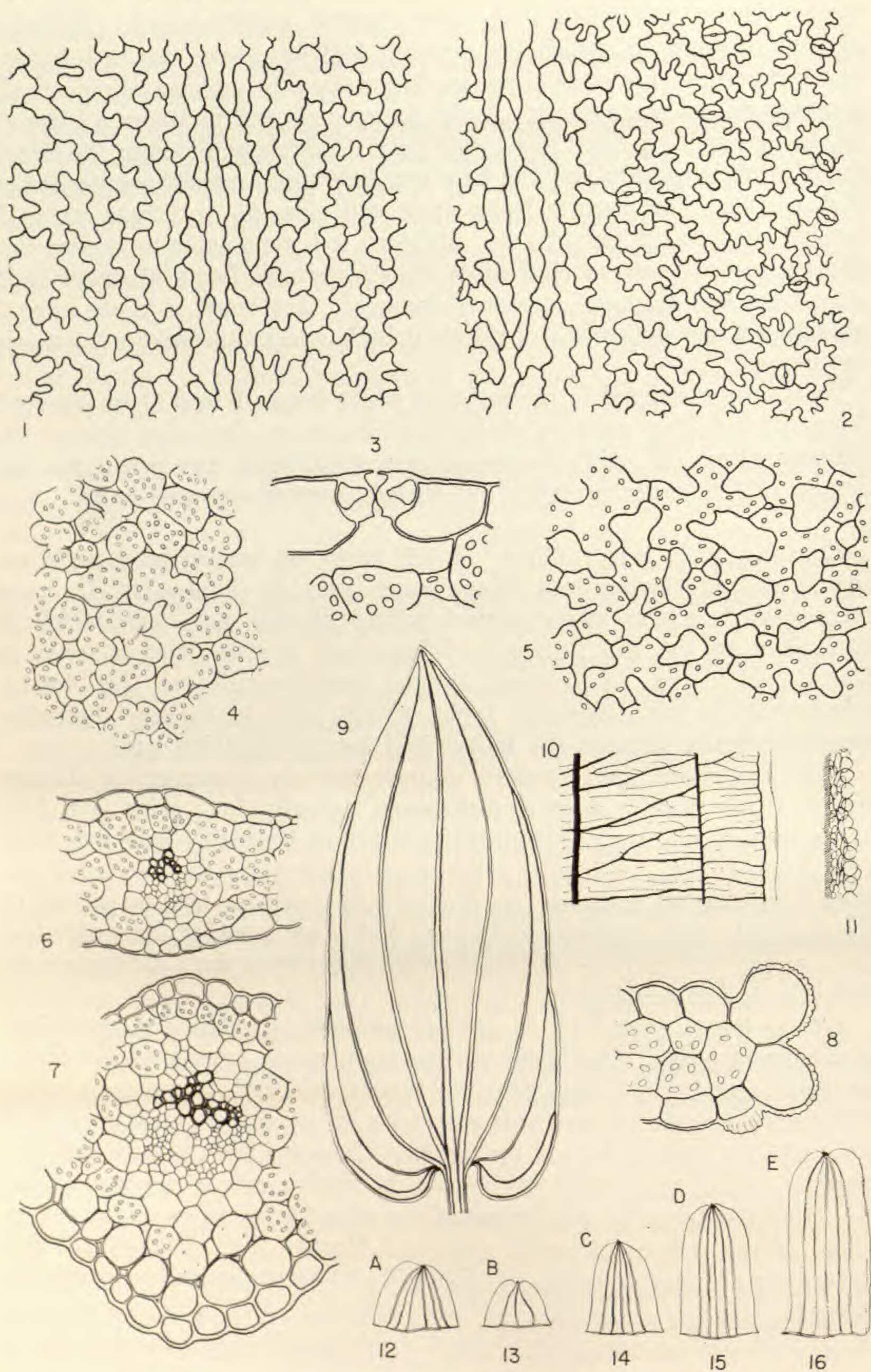
LEAVES. Scale leaves (FIGS. 12-16) borne on underground parts are readily distinguishable from foliage leaves borne on aërial parts. In many monocotyledons the morphological nature of the scale leaf, which is equivalent to the leaf base of a foliage leaf, is clear from a series of transitional leaves. In *Croomia*, without transitional leaves, this obvious relationship is lost. The two types of leaf seem to be very dissimilar developmentally because the foliage leaf has no sheathing base.

Scale leaves are open, opposite margins scarcely overwrapping. Leaves A and B are usually shortest with fewest (usually 3-4) veins (e.g. FIG. 13) whereas distal scales are longest and almost invariably have five veins (e.g. FIGS. 14-16). A regular progression in size along the rhizome is not always maintained, however (e.g. FIGS. 12-16), perhaps because growth of the renewal shoot is not continuous. Veins are parallel, converge and unite at the apex but are unconnected by transverse veins. A conspicuous mid-vein is not developed.

Foliage leaves (FIGS. 35, 36; 9) are petiolate but without a sheathing, encircling insertion. The blade has five major veins, prominent abaxially, the veins entering the blade from the petiole independently of each other. The outermost vein on each side gives off a marginal and two submarginal veins into the cordate base of the lamina. The veins unite in turn with the marginal commissure which itself joins the median vein at the apex (FIG. 9). Longitudinal veins are connected by an irregular series of transverse veins. Many minor transverse veins end blindly (FIG. 10), an unusual feature for a monocotyledon, not found in *Stichoneuron* and very rare in *Stemona*.

VEGETATIVE ANATOMY

LAMINA OF FOLIAGE LEAVES. Dorsiventral. Hairs absent. Cuticle thin on both surfaces. Epidermis moderately shallow, more or less uniformly thin walled, outer wall scarcely thickened. Adaxial epidermis (FIG. 1)



FIGS. 1-16, *Croomia pauciflora*. Leaf anatomy. FIGS. 1 and 2. Surface view of epidermis, $\times 100$. FIG. 1. Adaxial view. FIG. 2. Abaxial view. FIG. 3. Transverse section of stoma, $\times 470$, from abaxial epidermis of lamina. FIGS. 4 and 5. Mesophyll in paradermal view from cleared whole mount of lamina, \times

uniform in surface view, cells more or less isodiametric with markedly sinuous anticlinal walls; costal cells elongated, narrow and with less obviously sinuous but somewhat thicker walls than intercostal cells, the costal cells most distinct above and below large veins. Abaxial similar to adaxial epidermis except for numerous stomata (FIG. 2). **Stomata** anomocytic, 27–36 μ long, the stomatal pore apparently orientated at random. Each guard cell with a wide lumen, somewhat thickened towards the pore below the two more or less equal ledges (FIG. 3). Guard cells including numerous small chloroplasts. Marginal epidermal cells papillose, the outer wall distinctly striate (FIGS. 8, 11).

Mesophyll uniformly chlorenchymatous, 3–5-layered; mostly 3-layered at margin and becoming several-layered towards midrib and main veins. Mesophyll cells much lobed; adaxial layer (FIG. 4) relatively compact, but cells not anticlinally extended to form a distinct palisade; abaxial layer (FIG. 5) loose, much lobed, the intermediate mesophyll layers intermediate in extent of lobing; differences between successive mesophyll layers most evident in paradermal view (FIGS. 4 and 5). Chloroplasts appearing somewhat denser in adaxial as compared with abaxial mesophyll layers. **Veins** (vascular bundles) all alike apart from range in size, from small blind-ending veins to midrib (e.g. FIGS. 6 and 7); all separated from each epidermis by at least one layer of chlorenchyma. Largest veins (FIG. 7) resembling vascular bundles of petiole and with inconspicuously collenchymatous subepidermal layers below; small veins with reduced vascular tissues (FIG. 6). Veins inconspicuously sheathed by a single layer of elongated chlorenchymatous cells, without thick-walled sheathing layers except for cells below phloem with slightly thickened walls.

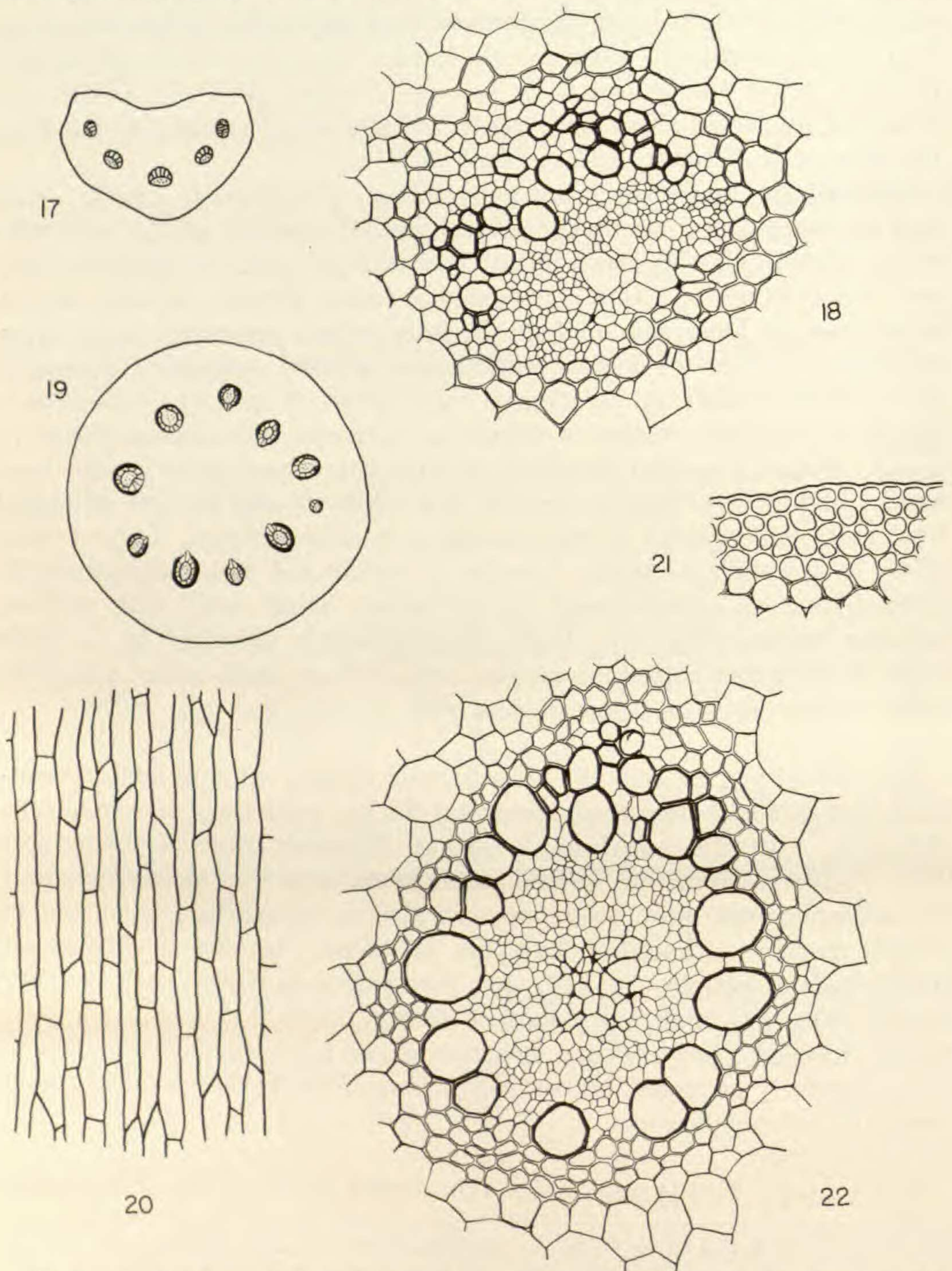
PETIOLE (FIGS. 17 and 18). **Epidermis** without sinuous walls, resembling that of aërial stem, with somewhat thicker walls than epidermal cells of lamina. **Cuticle** conspicuously striate. **Stomata** common. Outermost layer of chlorenchymatous ground parenchyma somewhat collenchymatous but **collenchyma** most conspicuous in abaxial hypodermal layer and in petiole margin. **Vascular bundles** collateral, usually 5 throughout greater part of petiole (FIG. 17), but 7 according to Holm; each vascular bundle (FIG. 18) with many narrow adaxial tracheal elements, the narrowest, adaxial (protoxylem) elements often partly occluded. Phloem with irregularly arranged, narrow sieve tubes. Bundle sheath cells usually distinctly collenchymatous.

SCALE LEAF. **Epidermal cells** thin walled, more or less rectangular

180. FIG. 4. Adaxial layer. FIG. 5. Abaxial layer. FIG. 6. Transverse section of minor vein of lamina, $\times 180$. FIG. 7. Transverse section of midrib, $\times 180$. FIG. 8. Transverse section of margin of lamina, $\times 290$. FIG. 9. Outline of lamina to show distribution of major longitudinal veins, $\times 1$. FIG. 10. Details of venation drawn from cleared whole mount of a leaf, midrib to left, $\times 3$. FIG. 11. Details of leaf margin from same preparation to show papillae, $\times 30$. FIGS. 12–16. Series of scales from rhizome, letters corresponding to nodes shown in FIG. 35; scales laid flat, $\times 1$.

in surface view. **Mesophyll** of uniform colorless parenchyma. **Veins** resembling major longitudinal veins of foliage leaf.

AËRIAL STEM (FIGS. 19–22). Stem more or less circular in transverse section, including up to 13 but usually 10 vascular bundles arranged in a

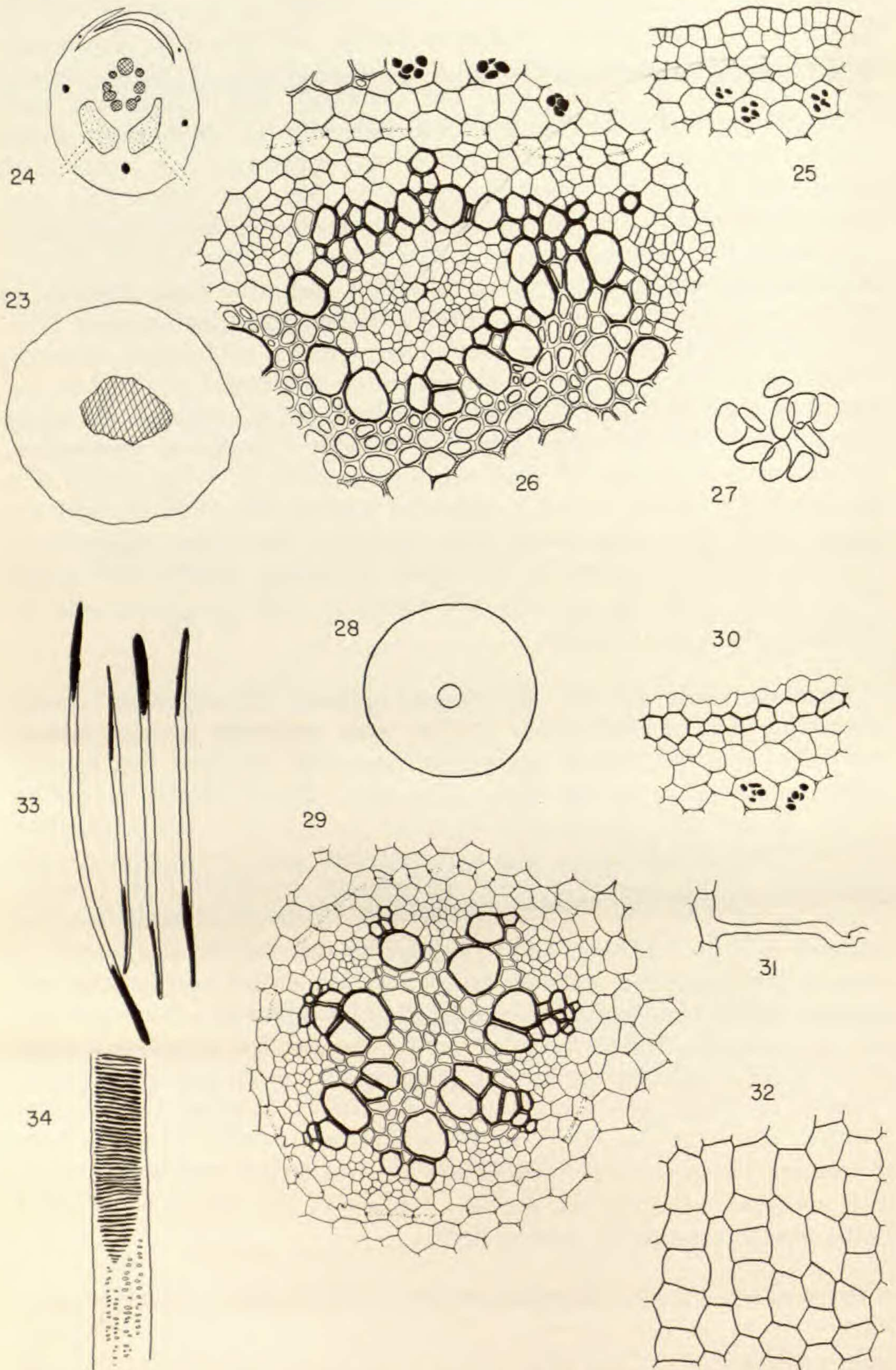


FIGS. 17–22, *Croomia pauciflora*. Anatomy of petiole and aërial stem. FIGS. 17 and 18. Petiole. FIG. 17. Transverse section, $\times 10$. FIG. 18. Transverse section of single collateral vascular bundle from petiole, $\times 180$. FIGS. 19–22. Aërial stem. FIG. 19. Transverse section, $\times 10$. FIG. 20. Epidermis, surface view, $\times 100$. FIG. 21. Surface layers of stem in transverse section, $\times 100$. FIG. 22. Transverse section of single amphivasal vascular bundle, $\times 180$.

circle (FIG. 19), the number of bundles increasing distally towards the insertion of foliage leaves. **Stomata** absent. **Cuticle** thin. **Epidermis** somewhat thick walled; epidermal cells longitudinally extended, more or less rectangular in surface view but commonly with oblique end walls (FIG. 20), normally colorless but basal cells with red (presumably anthocyanin-containing) vacuoles. **Cortex** with outermost 2–3 layers small celled and distinctly collenchymatous (FIG. 21), the collenchyma most pronounced distally; ground parenchyma otherwise uniformly large celled, thin walled, and colorless except for chloroplasts in outermost cells distally. Medullary ground parenchyma cells widest and with some tendency to collapse in a lysigenous manner. Each of largest vascular bundles (FIG. 22) amphivasal, including a continuous cylinder of tracheal elements, uniseriate except in region of narrow, often obliterated protoxylem elements on the inner side. Narrower vascular bundles collateral, the xylem discontinuous on the outer side and without conspicuous protoxylem. Phloem with inconspicuous sieve tubes surrounded by xylem and in turn surrounding a central strand of somewhat inflated cells (FIG. 22) with apparent wall thickenings which may represent obliterated protophloem. Vascular bundles sheathed by 2–3 layers of narrow, slightly thick-walled fibers or prosenchymatous cells, the sheath in large bundles usually incomplete next to protoxylem.

RHIZOME (FIGS. 23–26). **Epidermis** uniform, thin walled and closely resembling that of aerial stem. **Cortex** wide, uniformly parenchymatous and with abundant starch except for somewhat narrower but scarcely collenchymatous peripheral cells (FIG. 25). **Stele** angular in outline (FIGS. 23 and 24), delimited from cortex by a more or less continuous but indistinct endodermis of cells with suberized walls but without obvious Casparian thickenings (FIG. 26). Endodermis separated from vascular tissues by an indistinct 1–3-layered pericycle. Stele including an irregular cylinder of 9–10 indistinct and anastomosing vascular bundles forming a more or less continuous cylinder except for 2 somewhat more isolated and opposed lateral bundles. Additional small isolated phloem strands common next to pericycle. Larger vascular bundles more or less amphivasal (FIG. 26). Vascular cylinder enclosing a more or less continuous but irregular cylinder of fibers which often penetrate deeply between the vascular bundles. Sclerenchyma delimited internally by a further suberized layer resembling the peripheral endodermis, the two layers sometimes continuous via gaps in the vascular system. Medulla of thin-walled, starch-filled tissue resembling cortical ground tissue.

Root (FIGS. 28–32). **Epidermis** persistent but often collapsing somewhat; cells in surface view more or less rectangular, somewhat longitudinally extended (FIG. 32). Root-hairs uncommon, arising as outgrowths of otherwise unmodified cells (FIG. 31). **Exodermis** a compact layer of narrow, suberized, but scarcely thick-walled cells (FIG. 30). **Cortex** very wide, of uniformly starch-filled parenchyma with well-developed intercel-



FIGS. 23-34, *Croomia pauciflora*. Anatomy of rhizome and root. FIGS. 23-27. Rhizome. FIG. 23. Transverse section, $\times 10$, stele cross-hatched. FIG. 24. Diagram to show insertion of vascular tissues of lateral organs on rhizome. Leaf

lular space system; innermost cells somewhat wider than outermost. **Endodermis** inconspicuously differentiated from innermost cortical layer but small celled, thin walled and with conspicuous Casparian strips (FIG. 29). **Pericycle** uniseriate, thin walled, inconspicuous but usually distinguished from tissues within by its larger cells. **Stele** narrow (FIG. 28), polyarch with few (usually 6–7) xylem poles, the xylem arms irregular. Tracheal elements, together with central, thick-walled medulla, forming a fairly regular stellate core, the narrow, thin-walled phloem strands occupying the angles between the protoxylem poles (FIG. 29). Lateral roots are diarch with a more conspicuous endodermis according to Holm (1905).

CONDUCTING, STORAGE AND SECRETORY ELEMENTS. **Vessels** apparently restricted to metaxylem of roots (FIGS. 33 and 34); elements average 2 mm. long and $33\ \mu$ wide, each with long scalariform perforation plates on very oblique end walls up to $300\ \mu$ long, the thickening bars between the perforations (FIG. 34) scarcely thinner than those on very similar imperforated end walls of tracheids in other organs; lateral walls with scalariform pitting in areas of contact between adjacent vessels, otherwise walls with diffuse, narrow pits. Tracheal elements in rhizome often much longer than those in root; end walls scalariformly pitted but imperforate. Tracheids in aërial stem and leaves without definite end walls and with annular or spiral, rarely scalariform-reticulate wall thickenings, the thickening usually wound in one gyre. **Sieve tubes** in leaf, aërial stem and rhizome mostly with simple sieve plates on transverse to oblique but often rather indistinct end walls; sieve plates in sieve tubes of root compound, on oblique end walls.

Starch grains abundant in ground parenchyma of rhizome (FIG. 27) and root; grains up to $18\ \mu$ wide, ellipsoidal, flattened; hilum inconspicuous but not obviously excentric. Crystalline or other secretory products not observed.

COURSE OF VASCULAR BUNDLES

Early authors had included *Croomia* in the Berberidaceae because the morphology of its embryo was uncertain and the rhizome had been regarded as having a closed cylinder of wood. This was corrected by Gray

traces to subtending scale leaf C, solid black. Vascular masses of branch trace, stippled. Vascular bundles of rhizome stele cross-hatched. Traces to two roots attached directly to bud trace outlined with dotted lines. FIG. 25. Transverse section of surface layers, $\times 100$. FIG. 26. Transverse section of periphery of stele to show one large amphivasal bundle, $\times 180$. FIG. 27. Starch grains, $\times 400$. FIGS. 28–34. Root. FIG. 28. Transverse section, $\times 10$. FIG. 29. Transverse section of stele, $\times 180$. FIG. 30. Transverse section of surface layers, $\times 100$. FIG. 31. Longitudinal section of root hair, $\times 100$. FIG. 32. Epidermis from branch root, surface view, $\times 100$. FIG. 33. Isolated vessel elements, $\times 25$, extent of perforation indicated by solid black. FIG. 34. Details of vessel element, $\times 180$, lower limit of a perforation plate.

(1859). The vascular bundles which constitute the vascular system of the rhizome are certainly not obviously discrete but they are best revealed by tracing the changes in anatomy at nodes B and C where scale leaves, roots, and functional buds are inserted. The basic pattern is indicated diagrammatically in FIG. 24 which is constructed from serial sections through node C. The vascular system of the rhizome consists of an irregular series of larger strands alternating with smaller strands which are the traces to the scale leaves. These traces appear well below their exertion and pass gradually into the scale leaving a distinct "gap" in the main rhizome system. Two are usually conspicuous in a lateral position as indicated in the description of the rhizome. The bud trace system is a series of numerous isolated xylem and phloem strands which are aggregated into two large masses, each mass attached to a main rhizome strand. The middle trace of the subtending scale leaf passes between these two masses of bud trace tissue. Root traces may be attached directly to the branch system, others directly to large strands on the upper side of the rhizome. Beyond this complex nodal system there is a rapid change to the ring of discrete vascular bundles found in the erect stem, these bundles initially giving off traces to scales D, E and F. At the distal end of the aërial stem traces to foliage leaves and branches diverge shortly below the leafy shoot. There are no complicated nodal anastomoses such as have been described for *Stemona* by Lachner-Sandoval (1892).

REPRODUCTIVE MORPHOLOGY

GENERAL MORPHOLOGY (FIGS. 40-46). Flowers (FIGS. 40-44) are borne in long-stalked, few (1-3)-flowered cincinni (FIG. 46) in the axils of foliage leaves on vigorous shoots. Each flower is terminal on an axis bearing a single scale leaf (bracteole) which subtends the next flower-bearing axis. Each bracteole appears to be at right angles to the preceding one. Each pedicel has a distinct joint beyond the bracteole, representing a line of abscission. There are 4 green tepals in 2 pairs at right angles, the outer incompletely enclosing the inner (FIGS. 40-44). All tepals are somewhat reflexed in the open flower but in bud the apex of each, especially the inner pair, is distinctly hooded. The four stamens, each opposite a tepal, constitute a single whorl. Their bases are widened and united. In *Stemona* there have been attempts to interpret the stamens as forming two series so that they would correspond to the tepals, e.g. by Swamy (1964) who describes the stamen traces in *Stemona tuberosa* as diverging in pairs at different heights; but in this species Baillon (1860) showed the stamen primordia to arise simultaneously, as did Lachner-Sandoval (1892) in *Stemona javanica*. Each stamen (FIGS. 40-43) has a short fleshy filament, enlarged above, with two lateral 2-lobed thecae inserted somewhat obliquely and with latrorse dehiscence. Pollen grains are more or less spherical and with a finely reticulate surface (FIG. 45). The ovary is globular, unilocular, and appears to be unilocarpellate. It is grooved on one side only (the presumed ventral side (FIG. 42)). The placentation is unusual with

2-5 (usually 4) ovules all pendulous from an *apical* placenta below the short and inconspicuously 2-lobed stigma. However, the bitegmic ovules are irregularly anatropous so that the micropyle is directed upwards. The funiculus varies in length so that the ovules hang at varying heights in the loculus. A conspicuous feature of the funiculus is the mat of short, uniseriate hairs which later develop into the filamentous aril described and illustrated by Gray (1859). There are no nectaries but the epidermis on the inner surface of the tepals and of the filament and exposed part of the connective is papillose, the enlarged cells being densely cytoplasmic and filled with anthocyanin (FIG. 42).

VASCULAR ANATOMY (Figs. 47, 48). The vascular system of the flower is very simple (FIG. 47). Each tepal has five vascular bundles, a median and two pairs of laterals. All tepal bundles end blindly in a distal direction and never converge or anastomose although they may produce short, blind-ending branches. Each stamen has a single vascular bundle and the carpel has two. The vascular system of the flower arises from an irregular ring of narrow vascular strands, which may be regarded as a very reduced version of the system in the aërial axis. The way in which vascular strands initially diverge is not very uniform. The tepal and stamen traces arise first, the remaining central bundles aggregating to form the 2 bundles which irrigate the carpel. Tepal traces are small and collateral, each pair of laterals diverging from a common bundle; the median usually originates independently but sometimes diverges from the common bundle of one of its lateral pairs. The stamen trace most commonly diverges from the median trace to the corresponding tepal, less commonly it originates directly from the pedicel system, independently of the tepal traces. It may, however, diverge from the common bundle which produces 2 lateral tepal traces. The stamen trace is irregularly collateral with an admixture of phloem and xylem elements, most pronounced in the connective where the bundle is enlarged. There is no indication of the stamen appendage which is such a conspicuous feature of the flower of *Stemona*.

There is no difficulty in interpreting the vascular system of the ovary (FIG. 48) according to the classical theory of carpel morphology and its modern counterpart, which interprets the carpel as a conduplicate structure. One strand (the smaller) can be regarded as the dorsal bundle. It runs independently up one wall of the ovary into the stigma where it divides into 2 short procambial strands. In the opposite wall is the ventral bundle, beneath the distinct ventral groove. It bifurcates at the apex of the ovary, the two bundles constituting the vascular supply to the apical placenta. Each ovule is supplied by a branch from one half of this placental supply. The ovule trace ends in the funiculus, there being no vascular supply to the integuments, at least at the time of anthesis. There is no anatomical indication that either the dorsal or the ventral carpel bundle is a dual structure; in fact xylem and phloem are rather diffuse. The general configuration of this ovary recalls that of *Sarcandra* and other Chloranthaceae described by Swamy and Bailey (1950), except that in *Sarcandra*

the ovary has one ovule and the dorsal and ventral traces are most commonly double.

DISCUSSION

GROWTH HABIT. Our analysis of *Croomia* demonstrates that each unit of the sympodium has only two functional buds (the renewal bud and the dormant bud), the position of which is quite fixed. The rotation of one scale so that the renewal bud it subtends finds a position most favorable for continued growth is noteworthy. Of the two buds, one maintains the sympodium leaving only one to propagate the rhizome by branching. Even so, this is strongly inhibited and thereby the potential for vegetative propagation is reduced. It must be admitted that minute buds can be demonstrated, by microscopical methods, in the axils of other scale leaves. Their feeble vascular connection with the main vascular system of the rhizome, compared with that which connects functional buds to the main rhizome system, suggests that these obscure buds are vestigial. If propagation by seed is not vigorous the survival potential of *Croomia* must be low. This may well account for the relict status of the genus as indicated by its restricted and markedly disjunct distribution.

FLOWER. The morphology of the ovary calls for discussion since there seems to be lack of agreement in interpreting its structure in the related *Stemona* (cf. Baillon (1860) and Lachner-Sandoval (1892) on the one hand with Swamy (1964) on the other). It might be unwise to compare the ovary of *Croomia*, which has apical placentation, with *Stemona* which has basal placentation, but there are some notable anatomical similarities. It is unfortunate that *Stichoneuron* (with apical placentation) has to be excluded from this discussion but we have no comparable information about this genus.

Both Swamy and Baillon studied *Stemona tuberosa* Lour., Baillon using the name *Roxburghia gloriosoides* by which it was earlier known (Burkill, 1960). Lachner-Sandoval studied mainly *Stemona javanica* (as *Roxburghia javanica*), which has much smaller flowers, but he also investigated *Stemona tuberosa* (referred to as *Roxburghia gloriosa*) and does not comment on any major differences. The two early authors interpreted the carpel of *Stemona* as unicarpellate largely on developmental evidence. It originates as a single crescent-shaped protuberance opposite the first-formed tepal. This cushion of tissue grows in such a manner as to enclose the basal placenta. Swamy unfortunately had no access to this earlier information so his analysis based simply on the anatomy of the mature ovary is entirely original. He interpreted the ovary of *Stemona tuberosa* as bicarpellate because the ovules (up to 10) are in 2 rows. There are two identical vascular bundles in the ovary wall, one opposite each of the outer tepals. These Swamy regards as the dorsal bundles of 2 carpels, the ventral bundles being represented by the vascular supply direct to the basal ovules. In *Stemona javanica* according to Lachner-Sandoval, the two bundles in the

ovary wall are dissimilar, one bundle being double. This difference is most obvious in the dehiscent capsule, the line of dehiscence passing through the single bundle but between the double one. *Croomia* corresponds to *Stemona* in having 2 ovary bundles, one opposite each outer tepal. However, there is no indication of a bicarpellate condition since there is no reason to interpret these bundles other than as a dorsal and a ventral. Also the way in which the ovary is closed in the stigmatic region suggests a manner of development comparable to that described for *Stemona* by Baillon, although this speculation has not yet been verified. However, the great difficulty in comparing the ovaries of these two genera is the marked difference in placentation and consequently in placental vascular supply. In the absence of extensive comparative and developmental studies we must confess that the interpretation of the ovary of the Stemonaceae still remains open.

TABLE 1. Comparison of the three genera of Stemonaceae

	CROOMIA	STEMONA	STICHONEURON
HABIT			
General	erect herb	scandent	low shrub
Leaf arrangement	distichous	distichous, spiral or whorled	distichous
Longitudinal veins of lamina	diverging from base	diverging from base	some diverging from midvein
Free vein-endings in lamina	present	rarely present	absent
Rhizome	extensive	not extensive ?	not extensive ?
ANATOMY			
Hairs	absent	absent	uniseriate, thick-walled
Cauline and common bundles in stem internode	not distinct	distinct	distinct
Crystals	no raphides	raphides and styloids	raphides
Vessels in stem	absent	present	present ?
Sieve tubes in stem	sieve plates simple	sieve plates compound	sieve plates simple ?
REPRODUCTIVE PARTS			
Cincinni	few-flowered	few, many-flowered or flowers solitary	many-flowered (if a cincinnus)
Stamens	not appendaged	appendaged	not appendaged
Pollen	sculptured	smooth	sculptured ?
Ovary	unicarpellate	disputed	?
Placentation	apical	basal	apical
Aril	filamentous	vesicular	?

TAXONOMY. These morphological problems are compounded because in dealing with the three genera of the Stemonaceae it is not evident that they form a natural assemblage. Similarities between the genera are few but differences are many. The following features are common to them and diagnose the Stemonaceae. Flowers are somewhat perigynous and have: — two pairs of sepaloïd tepals, the outer pair at right angles to the inner; four stamens in a single whorl, one stamen opposite each tepal; a unilocular ovary with a short stigma. The ovules are anatropous, few to several, each with two integuments. The seeds are endospermous, ribbed and conspicuously arillate. The fruit is a 2-valved capsule. Leaves have a narrow insertion (not broadly encircling the stem) and a fairly characteristic cordate base. Stomata are anomocytic. The epidermis of the lamina has sinuous anticlinal walls. Some of the vascular bundles in the axis are amphivasal.

More detailed examination reveals marked differences which are set out, insofar as they are available, in TABLE 1. Even with this limited evidence it is clear that we are not dealing with a homogeneous assemblage. At this stage it would be presumptuous, therefore, to make any statements about the phylogenetic position of the Stemonaceae if it is suspected that they are an artificial group. A prior requisite to a correct understanding of their taxonomic status is the accumulation of a great deal more factual knowledge not only about them, but about their putative relatives.

SUMMARY

Shoots in *Croomia* are made up of units which branch sympodially. Each unit consists of a long-persistent rhizomatous portion and an annual erect, leafy shoot. The number of organs and their sequence, at least on the underground parts of the axis, is fixed within narrow limits. Only two functional vegetative buds are developed on the rhizome, a renewal bud which grows out immediately and a dormant bud which provides the only method of branching for the rhizome, although it is initially strongly inhibited. The anatomy of the vegetative organs and the flower is described. The simple vasculature of the ovary suggests that it is a single carpel despite its peculiar apical placentation. A summary of anatomical and morphological evidence suggests that *Croomia*, *Stemona*, and *Stichoneuron* constitute a rather heterogeneous assemblage.

ACKNOWLEDGMENTS

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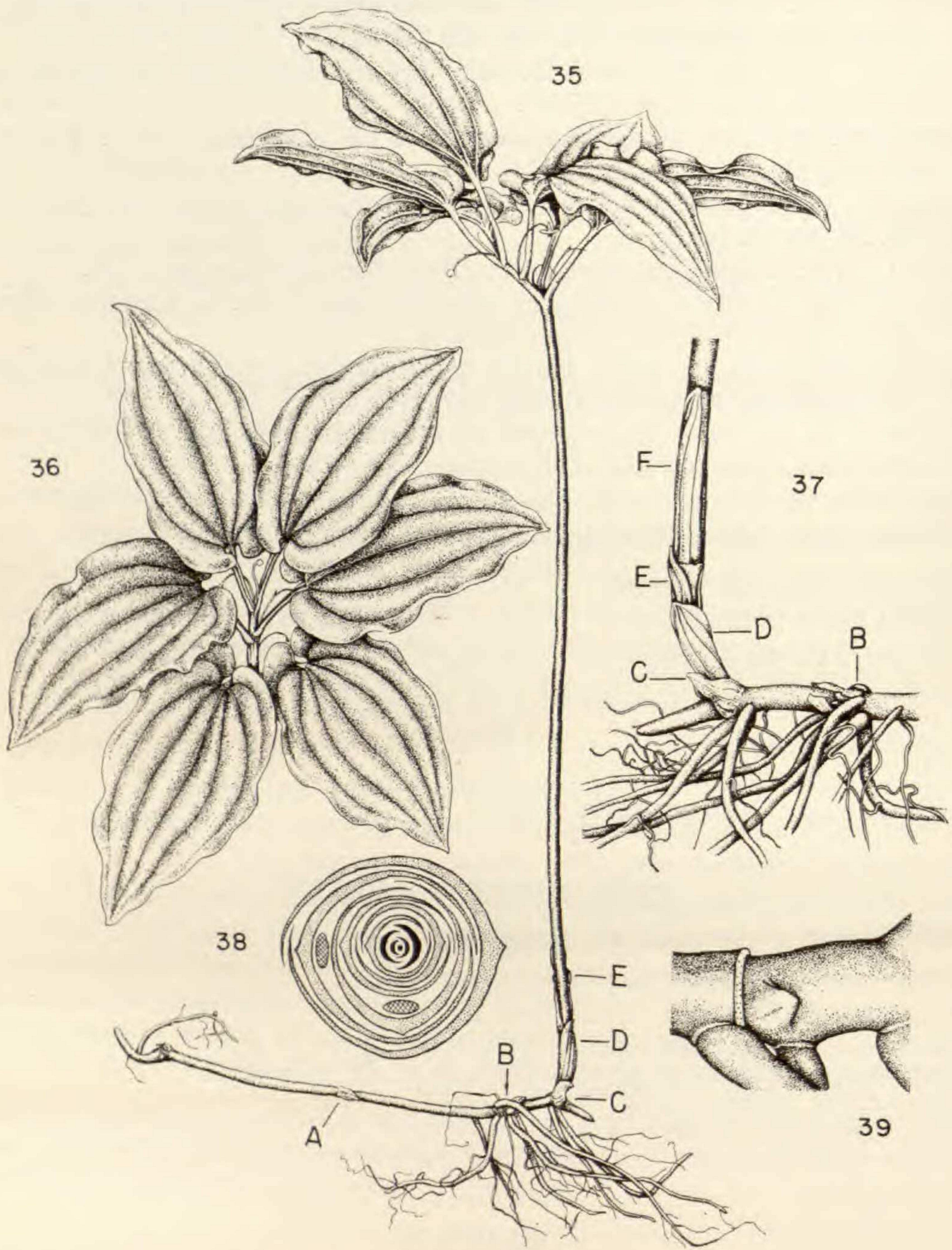
EXPLANATION OF PLATES

PLATE I

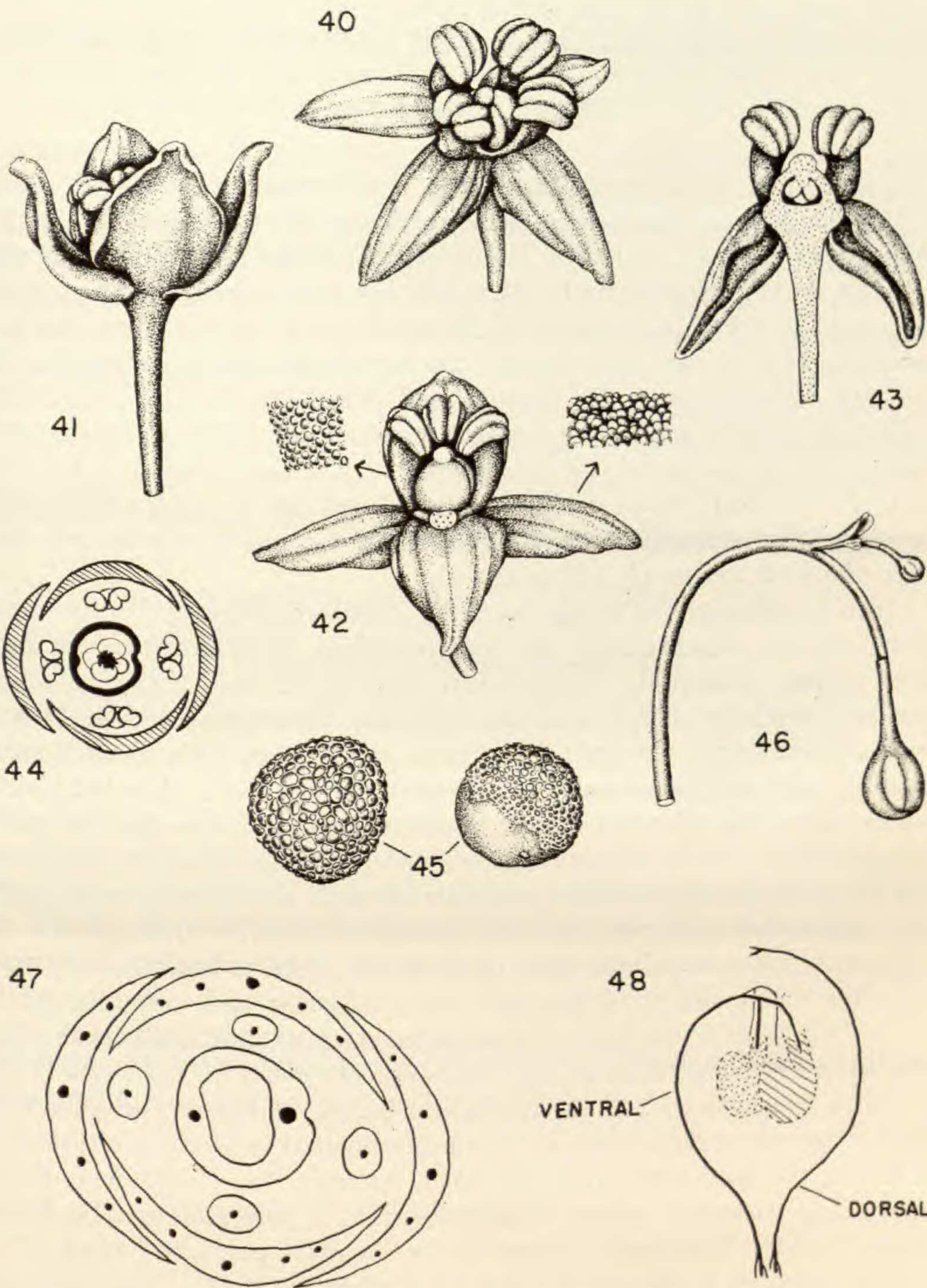
FIGS. 35–39, *Croomia pauciflora*, vegetative habit. FIG. 35. General habit of a plant in early April, $\times 1/2$. Scar of previous year's erect shoot on rhizome to left. FIG. 36. Leafy shoot from above, $\times 1/2$. FIG. 37. Details of base of erect shoot showing scales and renewal shoot, $\times 1$. FIG. 38. Diagram of growth unit in transverse section; scale leaves, stippled; foliage leaves, solid black; functional buds, cross-hatched. FIG. 39. Details of node B with scale-leaf removed to show dormant bud, $\times 3$. Letters A–F indicate successive nodes on early part of growth unit.

PLATE II

FIGS. 40–48, *Croomia pauciflora*, flowers. FIGS. 40–43. Open flowers in different aspects, $\times 4$. FIG. 40. Obliquely from above. FIG. 41. Lateral view. FIG. 42. Same, with one stamen cut off to show ovary. Insets: surface of filament (left), and adaxial surface of tepal (right), to show papillose epidermis. FIG. 43. Median section at 45° to dorsiventral plane of ovary. FIG. 44. Floral diagram. FIG. 45. Pollen grains, $\times 300$. FIG. 46. 2-flowered cincinnus, $\times 2$. FIGS. 47 and 48. Diagrams of vascular system of flowers. FIG. 47. Transverse section of flower constructed from several sections at different levels. Vascular bundles in solid black. FIG. 48. Ovary as seen in cleared flower, only 2 ovules shown.



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